12.—The Occurrence of Macropodidae on Islands and its Climatic and Ecological Implications

By A. R. Main*

Manuscript received—21st March, 1961

The islands of the western and southern coasts of Western Australia which support macropod marsupials have been formed by eustatic rise of the sea in post Pleistocene times; 15 of these islands support macropod marsupials. The smallest island supporting a population of macropods is only 240 acres in area. Two species are not found together in an insular situation until this is larger than 6 square miles in area. The problem of why only one species exists on islands 6 square miles in area or smaller is discussed in terms of past climate, time of isolation and inter-species competition. It is concluded that climatic differences at the time of isolation rather than inter-species competition probably account for the faunal differences in the Recherche Archipelago. Garden and Rottnest Islands are thought to be a clear cut case of competitive success of the tammar and quokka respectively. Outstanding problems which need further attention are mentioned.

Introduction

The more extensive geographical distribution of animal species during past times is commonly inferred from two sorts of evidence, fossil occurrences, and isolated populations occurring outside the principal present geographical range of the species.

In Western Australia fossil mammals have been studied by Glauert (1910, 1912, 1914, 1948) and Lundelius (1957). Obvious examples of the second type are island populations. There are 15 islands on the west and south coast inhabited by macropod marsupials (see Fig. 1). Such populations are of special interest for the following reasons:

(i) The islands were connected to the mainland during periods of lowered sea level at times of glacial advance during the Pleistocene. When glaciers melted and seas rose the islands were cut off from the mainland by the eustatic rise of the sea. Thus the origin of these insular populations can be precisely stated.

(ii) When the species found on the offshore island no longer occur on the adjacent mainland it can be inferred that the restriction of the main geographical range must have been later than the cutting off of the insular population.

(iii) The coastal islands arise from different depths of sea and if formed by eustatic rise in sea level cannot all be of similar age.

(iv) The coastal islands containing faunal relicts are of different size, geology, floristic or faunistic diversity. Thus the islands are a kind of field trial which has run over a relatively long period of time so that persistence of species can be measured against ecological factors in the environment. On most islands only one species of macropod is found, which suggests that a faunistic analysis in terms of inter-species competition would be possible.

The sizes of islands, and species occurring thereon, are listed in Table I.

The data of Table 1 raise two sorts of general problem, viz: (a) the order of island-size which will sustain one, two or three species, and (b) whether inter-species competition has operated to produce the single species populations which are characteristic of the smaller islands.

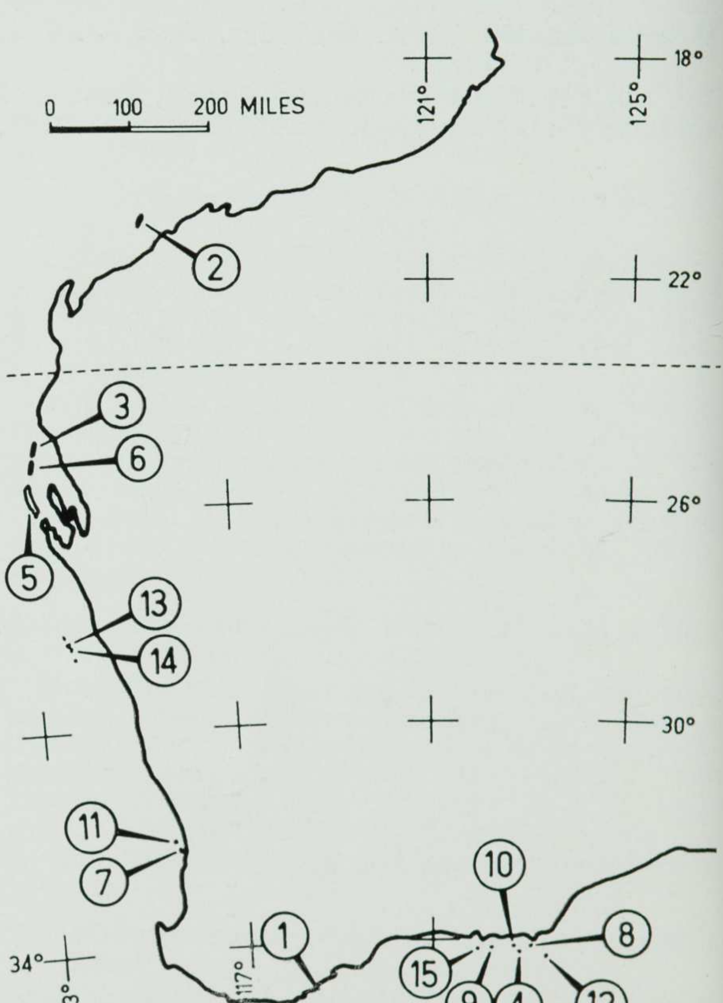

Fig. 1.—Locality map of islands referred to in text: 1 Bald; 2 Barrow; 3 Bernier; 4 Combe; 5 Dirk Hartog; 6 Dorre; 7 Garden; 8 Middle; 9 Mondrain; 10 North Twin Peaks; 11 Rottnest; 12 Salisbury; 13 Wallabi East; 14 Wallabi West; 15 Wilson.

*Zoology Department, University of Western Australia, Nedlands, Western Australia.

Island Size and Diversity of Habitat

There are numerous islands in the region under discussion which do not support macropods and are therefore not included in Table 1. Of these the majority are mere rocks or rookeries of sea birds. However, a few support a depauperate littoral or limestone flora and one or two species of reptiles, but no mammals; while an occasional island supports a small mammal species, e.g. Christmas (Recherche Archipelago) on which is found an *Isoodon* species. Not all of these islands can be regarded as small. Some e.g. North Island (Abrolhos) (940 acres) or Christmas Island (830 acres) are much larger than Combe Island (Recherche) (240 acres). It is probable that some of these islands may have originally contained a population of macropods which has not persisted. Confirmation of this suggestion is possible in some cases when skeletal remains are found, as at North Island (Storr 1960). There is no evidence that this extinction occurred during historical times. On the other hand it is difficult to envisage that such islands as Figure of Eight (Recherche), with bare rocky slopes, could have supported macropods although the island is more than twice the area of Combe.

Apart from island size, food and cover are important. Examination of Table 1 shows that neither the presence of trees nor great floral diversity is absolutely essential. Two of the Recherche islands (Boxer and Sandy Hook), 0.5 and 1.1 square miles in area respectively, have *Melaleuca* sp. and 87 and 100 + plant species respectively, but no macropods. Likewise the geology of the island, whether limestone or granite, does not appear to be of critical importance in determining which species of macropod is present except insofar as it provides the material for the tumbled piles of granite boulders utilised as cover by rock wallabies (*Petrogale*). During a recent visit to the island of the Recherche Archipelago Mr. R. D. Royce (personal communication) associated rock wallabies with those islands on which rectangularly jointed granite had produced a jumble of angular boulders which provided shelter in the form of "caves."

The eleven islands on which one species of macropod is found form a well-graded size series. Nevertheless Combe and Wilson are remarkably small compared with the larger islands of the series. The reality of the size break between Rottnest and Dorre needs confirmation on a more complete series of islands for it appears

TABLE I

Offshore islands, macropod present, size and ecological comment

Island	Area square miles	Macropod	Floral diversity *(No. of species)	Ecological	
				Trees	General
Combe	0·4	*Petrogale p. hacketti*	23	None	Granite boulders calcareous sand, saltbush flat
Wilson	0·5	*Petrogale p. hacketti*	37	*Melaleuca* 1 *Eucalyptus*	Granite dome
North Twin Peaks	1·1	*Protemnodon eugenii*	90	3 *Eucalyptus* *Melaleuca* *Acacia*	Granite gneiss no limestone
Salisbury	1·3	*Petrogale p. hacketti*	26	None	Granite and limestone. Shrubs only
Wallabi, East	1·4	*Protemnodon eugenii*	35	1 *Eucalyptus*	Coralline limestone and dunes
Wallabi, West	2·3	*Protemnodon eugenii*	31	No *Eucalyptus*	Coralline limestone lagoon deposit and dunes
Bald	3·0	*Setonix brachyurus*	85	*E. lehmanni Melaleuca*	Granite and coastal limestone
Mondrain	3·6	*Petrogale p. hacketti*	135+	4 *Eucalyptus*	Lacks limestone contains sand plain flora
Middle	4·2	*Protemnodon eugenii*	136+	4 *Eucalyptus* 2 *Melaleuca*	Granite, metasediments coastal limestone
Garden	4·5	*Protemnodon eugenii*	79	No *Eucalyptus*	Coastal limestone and recent sand dunes only
Rottnest	6·0	*Setonix brachyurus*	110	Formerly a Tuart (*Eucalyptus gomphocephala*) association *Melaleuca*, *Acacia*	Coastal limestone shell beds and recent dunes
Dorre	18	*Lagostrophus fasciatus* *Lagorchestes hirsutus* *Bettongia lesueuri*	98	3 *Eucalyptus* 2 *Acacia* *Heterodendron*	Sandstone and red sands some limestone
Bernier	18	*Lagostrophus fasciatus* *Lagorchestes hirsutus* *Bettongia lesueuri*	91	2 *Eucalyptus* 2 *Acacia* *Heterodendron*	Sandstones and red sands some limestone
Barrow	80	*Macropus robustus isabellinus* *Lagorchestes conspicaillatus* *Petrogale lateralis*	Not known		
Dirk Hartog	240	*Lagostrophus fasciatus* *Lagorchestes hirsutus* *Bettongia lesueuri*	66	2 *Eucalyptus* 6 *Acacia* *Heterodendron*	Sandstones and red sand with some limestone

* Islands of Recherche: data from Willis, J. H. (1953).—The Archipelago of the Recherche. 3a Land Flora. *Rep. Aust. Geogr. Soc.* No. 1 : 1–35 and from R. D. Royce (personal communcation).

that on islands between 6 and 18 square miles in area the environment becomes either extensive enough or sufficiently diverse for two or more species to co-exist. The examination of further islands intermediate in size between Rottnest and Dorre, perhaps within the Dampier Archipelago, would probably allow more accurate fixing of the smallest island which would contain two species. It would also be of interest to know whether the rock wallaby, tammar, and quokka are more similar in their ecological requirements and therefore more highly competitive than are the two hare-wallabies and the rat-kangaroo which co-exist on Bernier and Dorre.

Competition

The problems posed by the occurrence of single species on offshore islands has been long appreciated by local ecologists several of whom have attempted explanations. Clarke (1948, p. 141) accounted for the occurrence of the quokka (*Setonix brachyurus* (Q. & G)) on Rottnest and the larger tammar (*Protemnodon eugenii* (Desmarest)) on Garden Island as follows:

> *Setonix,* being physically inferior to *P. eugenii* would migrate to the end of the promontory [(formed by the rising seas) (the present Rottnest)] leaving *P. eugenii* in the Garden Island region. Subsequently the promontory was cut by the sea leaving the two species occupying different islands.

This interpretation obviates any consideration of inter-species competition but the concept of distribution being related to "physical inferiority" has no support as pointed out by D. L. Serventy (1951), who interpreted the present distribution of species on Garden Island and Rottnest as being the outcome of inter-species competition. V. N. Serventy (1953, p. 43-45) when discusing the mammal fauna of the Recherche Archipelago was presented with the problem of explaining the presence of different species (rock wallaby, *Petrogale penicillata hackettii* Thomas) and tammar on adjacent islands. He followed D. L. Serventy and accounted for the recorded distribution by postulating inter-species competition "based on Gauses' law" (p. 45). However, he adds that Dr. R. W. Fairbridge had pointed out that the depths recorded on the Admiralty charts showed that Mondrain, Salisbury, Combe and Wilson were separated from the mainland prior to Middle and North Twin Peaks. Thus the outer islands near the edge of the continental shelf may have been isolated for a considerable period before the inner islands closer to the present mainland and, as V. N. Serventy notes, environmental factors may have favoured one habitat or the other and thus favoured the rock wallaby or tammar on the two occasions.

Since the foregoing was writen much more is known of post Pleistocene climatic changes. Sea level changes can now be dated by means of radiocarbon dating (Godwin, Suggate and Willis 1958). The seas did not rise precipitately at the close of the glaciation (Godwin *et al.* op. cit.) and the periods when the first and last islands were isolated from the mainland are distantly separated in time (see Table II).

TABLE II

Islands of south coast and lower west coast of Western Australia, macropod present, and time of isolation

Island	Rising from sea, fathoms	Macropod	Time of isolation years (B.P.) approx.
Salisbury	45	*Petrogale*	15,000
Combe	33	*Petrogale*	12,500
Wallabi, East and West	29	*Protemnodon*	11,500
Wilson	27	*Petrogale*	11,000
Mondrain	25	*Petrogale*	10,500
Middle	18	*Protemnodon*	9,500
Bald	15	*Setonix*	9,000
North Twin Peaks	10	*Protemnodon*	8,000
Rottnest	5	*Setonix*	7,000
Garden	5	*Protemnodon*	7,000

From Table II it is apparent that *Petrogale* is restricted entirely to islands of the south coast older than 10,500 B.P. With the exception of the two Wallabi islands (11,500 B.P.) there is no overlap in age between those islands on which *Petrogale* occurs and those in which *Protemnodon* or *Setonix* are found. There are thus two problems (i) the apparent anomaly in the age and fauna of the Wallabi islands and (ii) the possible explanation for the almost complete separation of the islands of Table II into an older and a younger group with different faunas.

From present day distributions of the three species it is clear that *Petrogale* occupies the climatically drier environment (Table III). Thus the presence of *Petrogale* on islands older than 10,500 years suggests that such islands were isolated in a drier climatic period than the more recent islands. Mainland occurrences of *Petrogale* suggests that drier climate must be accompanied by rock outcrops and rock shelter to provide a suitable habitat. Such environmental prerequisites are not present on either East or West Wallabi islands in which case it is possible that *Protemnodon,* relieved of competition with *Petrogale* may have extended its range into a drier environment in which it was later isolated by rising seas. Such an hypothesis would explain the apparent anomaly in the macropod fauna of the Abrolhos. However, it also clearly indicates that further work on the biota of these islands is necessary.

The broader implications of the data of Table II centre around the question of whether at the time of the more recent isolation, the climate was similar to that of the earlier isolation. If it was not, the events which led to the persistence of different species on the earlier and later isolated islands would not be similar and the end result (different species on each island) is not comparable in terms of a field experiment in competition.

The problem can be stated another way; it is desired to distinguish between the two following possibilities:

(a) That two species occurred simultaneously in the same area (zone of overlap, see below).

(b) That two species occurred chronologically in the same area. In their mainland distribution the three species (quokka, tammar, and rock wallaby) are essentially allopatric. In regions of overlap they are separated by marked habitat preferences. Under these conditions it is difficult to envisage that inter-species competition occurs. On islands, however, species do occupy habitats that differ remarkably from that preferred on the mainland, e.g. on Rottnest the quokka occupies shrub steppe while on the mainland it is restricted to swamp thickets. Data for all three species are summarised in Table III.

It is conceivable that two species could have been in the same general area (zone of overlap) and were cut off together on the same island. In this case we might expect to find islands of similar age with different species, e.g. Rottnest and Garden Islands. Should the presence of rock shelter prove to be the controlling factor for the rock wallaby then, from the fact that some islands are now inhabited only by rock wallabies, one cannot infer that the tammar did not occur in the vicinity during the past. Among the islands of the Recherche, however, there is, as already noted (Table II), complete separation of the island fauna into an older with *Petrogale* and a younger with *Protemnodon*. This argues against co-existence (zone of overlap) prior to island formation and suggests a climatic change betwen the isolation of the older and younger islands. Should the climate have become wetter than previously the tammar may have replaced the rock wallaby on the mainland and tammar would be included in the fauna of any islands subsequently formed in this area.

In Europe and North America the close of the Pleistocene was marked by a number of climatic oscillations and it would not be surprising if similar changes marked the end of the Pleistocene in Australia. The older and younger island faunas discussed above would represent one oscillation.

The sorts of changes in the atmospheric circulation which could produce such climatic changes can be discussed in terms of theoretical meteorological concepts (Willett 1953) and it is instructive to do so in the present case in order to see whether the theory predicts a change

TABLE III

Preferred environmental conditions as indicated by habitat occupied throughout the present mainland occurrence, contrasted with the environments present on the islands where animals are now abundant

Species	Mainland	Island
Setonix brachyurus	Permanently wet swamps which do not dry in summer. Vegetation provides deep cool shade, grows throughout year and provides dense cover.	*Rottnest*—Dry steppe-like arid situation produced under grazing climax. Vegetation markedly seasonal in growth, provides little shade or cover. Water limited during summer. *Bald*—Similar to adjacent mainland; dense patches of vegetation growing continuously due to persistent rains.
Protemnodon eugenii	Not known to occur in wetter south-west, limited to thickets in the sclerophyllous woodland savannah woodland, and shrub woodlands	*Garden*—*Acacia* thickets with *Callitris* and *Melaleuca*—no free water. *North Twin Peaks*—*Eucalyptus*, *Acacia acuminata Melaleuca*, *Callitris*—? no free water. *Middle*—Granite, metasediments, coastal limestone *Eucalyptus* and *Melaleuca*. *Wallabi (East and West)*—*Eucalyptus*, *Acacia*, no permanent fresh water.
Petrogale pennicillata hacketti	Rocky and precipitous hills of granite or metasediments with boulders or caves in the shelter of which the animal retreats during the day. In savannah woodland and sclerophyllous woodland and communities on the dry side of these. Does not appear to be dependent on free water.	*Wilson*—*Eucalyptus*, *Agonis*, *Melaleuca* and *Astartia*. Forming thickets on the north and east side of high granite area. South side predominantly wind planed shrubs, *e.g.*, *Leucopogon*, *Beyeria*, *Pimelia* and *Calocephalus* and *Carpobrotus*. Mostly rocky with sparse patches of soil. *Mondrain*—Granite, lacks limestone; has *Eucalyptus*, *Acacia*, *Melaleuca*, *Casuarina huegeliana*, patches of heathland = isolate of mainland habitat. *Combe*—Sandy over granite with granite boulders; is a saltbush (*Atriplex*) flat. *Salisbury*—Granite headland plus consolidated Pleistocene beach dunes (= aeolianite). Shrubs or dense thickets up to 5 feet high.

from a dry to wet about the time of isolation of the younger (tammar) islands in the Recherche.

Possible Climatic Change

Meteorologists have been struck by the similarity of the climate at the time of glacial advance and retreat to the index cycle (for description see Rossby and Willett 1948). Willett (1948) points out that an ice age is like a low index pattern while an interglacial is like a high index pattern.

Craig and Willett (1951, p. 383) further discuss the index cycle. They point out that the passage from a high to a low index is characterised by the splitting of cyclones and anticyclones with predominantly east-west orientation of the major axis into centres of action with north-south orientation. "The result is an increase of latitudinal exchange of air masses and storminess and of extreme air mass contrasts in lower middle latitudes." They conclude (p. 389). "These considerations suggest that glacial epochs, stages and sub-stages, periods of climatic stress such as the sub-atlantic period and stormy centuries result from the predominance over various periods of time of low index conditions . . ."

There is geological evidence from both Europe and North America that during the last 20,000 years glaciers retreated and advanced several times. These alterations in the ice sheet have been dated by means of radiocarbon dating and are summarised in tabular form by Emiliani (1955), Horberg (1955) and Wright (1957). From these data it seems that periods of retreat were reversed between 14,000-12,000 B.P. and again about 11,000 B.P. At about 10,750 Wright (from Gross 1954) cites the climate as being "very cold, maritime subarctic" (previous cold periods being continental). This climate corresponds with the Fennoscandian stage of Europe and the Mankato of North America. Presumably the climate of Europe was marked by an extreme development of the low index cycle. The glacial climates have always been parallel in both hemispheres, and it seems likely that this extreme low index cycle was world wide.

From Table II it is apparent that in the Recherche Archipelago, islands isolated prior to about 10,500 contain *Petrogale* while those isolated later have *Protemnodon*. *Protemnodon* prefers a wetter environment with assured winter-type rainfall of 90-150 wet days a year and it seems possible that it extended its range eastward into a region formerly occupied by *Petrogale* which was becoming wetter because of the greater storminess of a low index period. Thus change in the climate deduced from glacial happenings agrees with the change in species isolated on the more recently formed islands of the Recherche and the agreement is thought not to be coincidental.

Discussion and Conclusions

The data presented suggest that it is possible to establish the minimum area necessary for the natural containment of one species of small macropod. It also suggests the order of the island area necessary for containing two species. A field investigation of diet in these minimal areas may perhaps reveal that some animals are leading a marginal existence. This aspect should be investigated.

The dating of sea level rises supports the suggestion of Fairbridge (in Serventy 1953), and shows that the occurrences of different species on adjacent islands of the Recherche Archipelago need not necessarily reflect the outcome of inter-species competition. The interpretation is based on the usual biogeographical assumption that animals (tammar and rock wallaby) which are now essentially allopatric will also have been separated in the past.

On Bald Island competition may have operated but we have insufficient data on which to say whether at the time of isolation only the quokka was present or whether both tammar and quokka occurred. Most probably both were present and competition eliminated the tammar.

On the west coast both tammar and quokka are present on the mainland and almost certainly were present together when Garden and Rottnest were isolated. The present distribution appears clearly interpretable in terms of inter-species competition as already interpreted by D. L. Serventy (1951). In the case of East and West Wallabi there are no data on which to assert that the quokka was present, as well as the tammar, when these islands were part of the mainland. Thus it is not possible to infer that competition was the cause of the present distribution.

Since the various islands apparently are not of comparable age the taxonomic concepts of the species and sub-species status of the various insular and mainland populations should be reinvestigated, in particular, as noted by Tate (1948), the disposition of the Garden Island and Wallabi Island tammars in the same sub-species and different from the mainland one. See also Glauert (1934) and Troughton (1941), each of whom has a different arrangement.

Acknowledgements

The author acknowledges receipt of a University Research grant while the work reported in this paper was in progress. Visits to Bald Island and the Abrolhos were financed from portion of a grant made by The Commonwealth Scientific and Industrial Research Organisation to Professor H. Waring for Marsupial Studies.

Assistance was given from many quarters: Mr. Jack Westerberg of Albany provided transport to Bald Island and echo sounding data of the depth of the channel; Messrs. Harry Ackerstrom and Clive Willock provided hospitality on the West Wallabi Island and the echo sounding data of the depth of Geelvink Channel; Mr. G. M. Storr assisted in the field and provided the figure of the number of plant species on Bald Island; and Mr. R. D. Royce, Chief Government Botanist, identified plant specimens and provided species lists for Recherche, Bernier and Dorre Islands. The Department of Primary Industry Fisheries Division (Canberra) gave permission for Mr. Royce and Mr. G. Brown to accompany Dr. R. W. George when he visited the Recherche Archipelago during a Commonwealth charter to assess commercial possibilities of the southern crayfish in Western Australia. Dr. George and Messrs. Royce and Brown made their field notes available to the author. Data on the ocean depths in the Recherche Archipelago were supplied by Messrs. Poole Brothers. The Golden Gleam Canning Co. of Geraldton and Mr. A. J. Fraser, Director State Fisheries Department, provided transport to the Abrolhos on separate occasions.

Professor H. Waring and Messrs. J. H. Calaby and R. D. Royce read and criticised the manuscript.

References

Clarke, J. R. (1948).—Anatomy of the quokka [*Setonix brachyurus* (Quoy & Gaimard)] Part 1.—External morphology and large intestine. *J. Roy. Soc. W. Aust.* **33**: 59-150.

Craig, R. A., and Willett, H. C. (1951).—"Compendium of Meteorology." pp. 379-390. (Ed. T. F. Malone.) (Amer. Met. Soc.: Boston.)

Emiliani, C. (1955).—Pleistocene temperatures. *J. Geol.* **63**: 538-578.

Glauert, L. (1910).—*Sthenurus occidentalis* (Glauert). *Bull. Geol. Surv. W. Aust.* **36**: 53-69.

——— (1910).—The Mammoth Cave. *Rec. W. Aust. Mus.* **1**: 11-13.

——— (1912).—The Mammoth Cave (continued). *Rec. W. Aust. Mus.* **1**: 39-46.

——— (1914).—The Mammoth Cave (continued). *Rec. W. Aust. Mus.* **1**: 244-248.

——— (1934).—The distribution of marsupials in Western Australia. *J. Roy. Soc. W. Aust.* **19**: 17-32.

——— (1948).—The Cave Fossils of the South-West. *W. Aust. Nat.* **1**: 100-104

Godwin, H., Suggate, R. P. and Willis, E. H. (1958).—Radiocarbon dating of the eustatic rise in ocean-level. *Nature, Lond.* **181**: 1518-1519.

Gross, H. (1954).—Das Alleröd-Interstadial als Leithorizont der letzten Vareisung in Europa und Amerika. *Eiszeitalter u. Gegenwart* **4/5**: 189-209.

Horberg, L. (1955).—Radiocarbon dates and Pleistocene chronological problems in the Mississippi Valley Region. *J. Geol.* **63**: 278-286.

Lundelius, E. (1957).—Additions to knowledge of the ranges of Western Australian mammals. *W. Aust. Nat.* **5**: 173-182.

Rossby, S. G. and Willett, H. C. (1948).—The circulation of the upper trophosphere and lower stratosphere. *Science* **108**: 643-652.

Serventy, D. L. (1951).—Inter-specific competition on small islands. *W. Aust. Nat.* **3**: 59-60.

Serventy, V. N. (1953).—The Archipelago of the Recherche Part 4 Mammals. *Rep. Aust. Geogr Soc.* No. 1: 40-48.

Storr, G. M. (1960).—The physiography, vegetation and vertebrate fauna of North Island, Houtman Abrolhos. *J. Roy. Soc. W. Aust.* **43**: 59-62.

Tate, G. H. H. (1948).—Results of the Archbold Expedition. No. 59. Studies on the anatomy and phylogeny of the macropodidae (marsupialia). *Bull. Amer. Mus. Nat. Hist.* **91**:239-351.

Troughton, E. (1941).—"Furred Animals of Australia." (Angus & Robertson: Sydney.)

Willett, H. C. (1948).—Patterns of World Weather Changes. *Trans. Amer. Geophys. Un.* **29**: 803-809.

——— (1953).—"Climatic Change." pp. 51-71. (Ed. H. Shapley.) (Harvard Univ. Press: Cambridge.)

Wright, H. E. (1957).—Late glacial chronology of Europe—A discussion. *Amer. J. Sci.* **255**: 447-460.